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The Asian part of Turkey, i.e. Anatolia, is the region where three of the world's 35 biodiversity hotspots meet, and interact: the Caucasus, Irano-Anatolian, and Mediterranean basin hotspots. One of the most distinctive biogeographic features that helps in understanding the biodiversity of Anatolia is the Anatolian diagonal, which has long been recognised as a biogeographic boundary between the central and eastern Anatolian floras and faunas, but the processes (i.e. historical, ecological or some combination of these) responsible for its origin and maintenance have not been well understood. The aim of this study was to assess whether the Anatolian diagonal corresponds with a significant environmental barrier. I used for this purpose ecological niche modelling and associated comparative metrics. First, I created virtual records in the Anatolian part of the Irano-Anatolian hotspot, and split these records into two groups: those occurring to the west and to the east of the Anatolian diagonal. Then, I examined whether the Anatolian diagonal is associated with a steep environmental gradient. It was found that the Anatolian diagonal is indeed associated with a steep environmental gradient, and therefore corresponds with a significant environmental barrier. This steep gradient associated with the Anatolian diagonal is mainly in temperature seasonality. The models did not cross-predict each other, either at the Last Glacial Maximum or at the present, suggesting that during at least the last glacial-interglacial cycle, many of these populations or taxa were excluded from the other side of the Anatolian diagonal by environmental rather than non-environmental reasons (i.e. dispersal, competition).

Keywords: Anatolia; Anatolian diagonal; biodiversity hotspot; ecological niche modelling; environmental barrier; niche

Introduction

The Asian part of Turkey (Anatolia) is the region where three of the world's 35 biodiversity hotspots meet, and interact: the Caucasus, Irano-Anatolian, and Mediterranean basin hotspots (Mittermeier et al., 2004). While Anatolia has a high level of biodiversity and a high percentage of life found nowhere else on the planet, it has lost most of its original natural vegetation (Conservation International, 2015). This high biodiversity and rate of endemism in Anatolia (e.g. of over 9000 known native vascular plant species, one third is endemic) is thought to result from its location at the nexus of Europe, the Middle East, Central Asia, and Africa and its high topographic and climatic heterogeneities. However, over the previous millennia, human activities have dramatically changed the terrestrial ecosystems of Anatolia, one of the earliest loci of human civilization (Şekercioğlu et al., 2011).

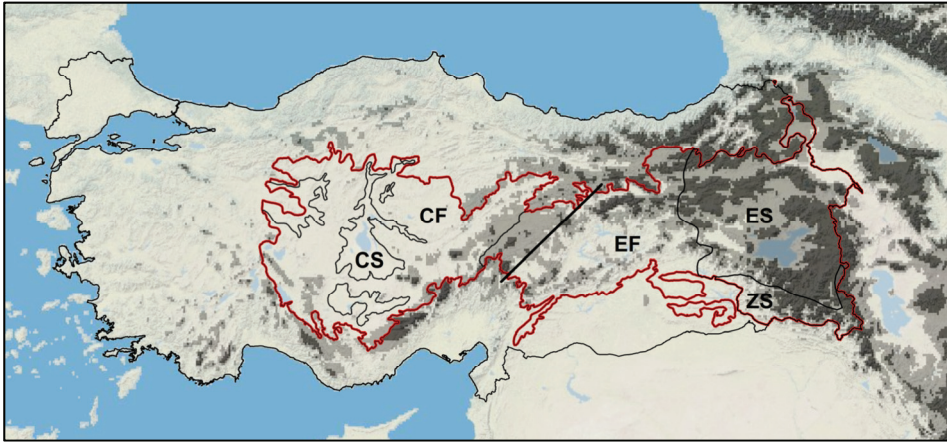
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Figure 1. Map of the study area showing Turkey (black line) and the Anatolian part of the Irano-Anatolian hotspot (red line). The Anatolian part of the Irano-Anatolian hotspot hosts five different ecoregions (CS: Central Anatolian steppe; CF: Central Anatolian deciduous forests; EF: Eastern Anatolian deciduous forests; ES: Eastern Anatolian montane steppe; ZS: Zagros Mountains forest steppe). The thick black line indicates the approximate midline position of the Anatolian diagonal, and the shaded area elevation (light grey: <1500 m; dark grey, 1500–2000 m; black, >2000 m).

One of the most distinctive biogeographic features that helps in understanding the biodiversity of Anatolia, and has received increased attention in recent years is the Anatolian diagonal. It was discovered by J. Cullen, and first referred to by Davis (1971), based on the distribution patterns of plant species in the first volume of the "Flora of Turkey and the East Aegean Islands". Ekim and Güner (1986) reaffirmed the Anatolian diagonal, based on the distribution patterns of plant species in the first eight volumes of the "Flora of Turkey". The Anatolian diagonal runs from the northeast of Turkey (i.e. from the vicinity of Bayburt-Gümüşhane) to the southwest, where it splits into two branches toward the Mediterranean, one through the Amanos Mountains and the other through the Central Taurus Mountains. It divides inner Anatolia, covered by the western part of the Irano-Anatolian hotspot (hereafter referred to as the Anatolian part of the Irano-Anatolian hotspot; Eken et al., 2004; Conservation International, 2015), into two regions (i.e. central lowland Anatolia, mainly <1500 m, and eastern highland Anatolia, mainly >1500 m) with different faunistic or floristic communities (Davis, 1971; Ekim & Güner, 1986; Welch & Kirwan, 2008), one including the "Central Anatolian steppe" and "Central Anatolian deciduous forests" ecoregions and the other including the "Eastern Anatolian deciduous forests", "Eastern Anatolian montane steppe", and "Zagros Mountains forest steppe" ecoregions (Welch & Kirwan, 2008; Figure 1).

The Anatolian diagonal acts as a barrier to dispersal for, and therefore coincides with the distributional limits of, many populations (e.g. lineages, Rokas, Atkinson, Webster, Csoka & Stone, 2003; Gündüz et al., 2007; Mutun, 2010; Vamberger et al., 2013; Korkmaz, Lunt, Çıplak, Değerli & Başıbüyük, 2014) or taxa (e.g. species or subspecies, Davis, 1971; Ekim & Güner, 1986; Nilson, Andren & Flardh, 1990; Çıplak, Demirsoy & Bozcuk, 1993; Adıgüzel, 1999; Demirsoy, Salman & Sevgili, 2002; Çıplak, 2003; Doğan, Duran & Hakkı, 2009; Stümpel & Joger, 2009; Bilgin, 2011; Uslu, Bakış & Babaç, 2011; Uslu & Bakış, 2012; Kapli et al., 2013; Sonibare et al., 2014). For example, many of Turkey's 1200 endemic plant species occur only to the

immediate west or east of it (Conservation International, 2015 and references therein). Moreover, the Anatolian diagonal is suggested as contributing to regional historical-cultural differences (Aydın, 2004).

Although the Anatolian diagonal has long been recognised as a biogeographic boundary between central and eastern Anatolian floras and faunas, the processes (i.e. historical, ecological or some combination of these) responsible for its origin and maintenance have not been well understood. According to Davis (1971), this biogeographic boundary cannot be explained by physical and climatic differences between the west and east of the Anatolian diagonal, and has roots from the palaeogeological (Coenozoic) history of Anatolia. However, Ekim and Güner (1986) suggested that ecological and climatic factors may play some greater role than previously understood (see also Avcı, 1993). I therefore tried to assess whether the Anatolian diagonal corresponds with a significant environmental barrier. For this purpose, I used ecological niche modelling (Elith & Leathwick, 2009) and associated comparative metrics (Warren, Glor & Turelli, 2010; Glor & Warren, 2011). I created virtual records in the Anatolian part of the Irano-Anatolian hotspot, and split these records into two groups using the Anatolian diagonal. Then I examined whether the Anatolian diagonal is associated with a steep environmental gradient.

Material and Methods

Virtual Records To make sure that the results were not influenced by the choice of populations (e.g. lineages) or taxa (e.g. species or subspecies) and the peculiarities thereof, and also to obtain an unbiased dataset, virtual records were created by randomly sampling a set of records (i.e. a set of geographic localities, with latitude and longitude coordinates) in a given habitat throughout a given region (see Kramer-Schadt et al., 2013; Fourcade, Engler, Rodder & Secondi, 2014 for a similar approach). To reduce spatial autocorrelation (Boria, Olson, Goodman & Anderson, 2014), only one record was allowed to occur within a grid cell of 0.083 decimal degree^2 (c. 100 km^2). Eventually, 200 records or geographic localities were extracted from areas covered by herbaceous or shrubby (i.e. steppe or anthropogenic steppe) vegetation (i.e. "Open Shrubland", "Grassland", and "Cropland" categories of UMD Global Land Cover Classification, http://glcf.umd.edu/data/landcover; Hansen, DeFries, Townshend & Sohlberg, 1998) within the Anatolian part of the Irano-Anatolian hotspot (Biodiversity Hotspots Arcview Shapefile and Metadata, www.cepf.net/resources/hotspots). It is important to note that only a small part of the Anatolian part of the Irano-Anatolian hotspot is covered by other vegetation types. These records were then split into two groups: those occurring in the west (hereafter referred to as group A) and east (hereafter referred to as group B) of the Anatolian diagonal and allowed to meet along it, resulting in 85 and 115 records for group A and B, respectively, used for modelling. Thus, group A and B are distributed in steppe or anthropogenic steppe habitats throughout the Anatolian part of the Irano-Anatolian hotspot (Figures 2, 3), and cover the full range of different climates to the west and east of the Anatolian diagonal, respectively.

Environmental Data. Present (1950–2000) and Last Glacial Maximum (LGM, about 22,000 years ago) environmental data as well as elevation data were obtained from the WorldClim database (www.worldclim.org; Hijmans, Cameron, Parra, Jones & Jarvis, 2005) at a resolution of 2.5 arc-min. Environmental data include 19 bioclimatic variables derived from monthly temperature and precipitation values (see www.worldclim.org/bioclim for detailed descriptions of these variables). LGM environmental data are based on a Global Climate Model (GCM) simulation: the Max Planck Institute for Meteorology (MPI-M), the new Earth system model (MPI-ESM-P; see CMIP5-Coupled Model Intercomparison Project Phase 5, http://cmip-pcmdi.llnl.gov/cmip5 for details). All variables were masked to include only 25° to 47°E and 35° to 43°N, and then tested for multicollinearity. Some highly intercorrelated (r > 0.80 or < -0.80) variables were removed (Dormann et al., 2013), leaving elevation and BIO2-4, 8-10, 12, 15, and 18-19 as input variables used for modelling.

Modelling. To develop the ecological niche models for group A and B, a maximum entropy machine learning algorithm available in the software MAXENT version 3.3.3 k (www.cs.princeton.edu/~schapire/maxent; Phillips, Anderson & Schapire, 2006; Phillips & Dudik, 2008) was used, together with virtual records and environmental data. The models were developed under present (1950–2000) environmental conditions, and then projected to LGM (about 22,000 years ago) environmental conditions. MAXENT was run with the default settings, except for the cases noted below. To evaluate how each bioclimatic variable affected the prediction, the response curves were created. To estimate the relative contributions of bioclimatic variables to the model, the jack knife analysis was conducted. To test whether the model performance was robust to variation in the selection of the records for training and testing, a ten-fold cross-validation was performed. To examine the effect of the region used for modelling, two models were run for each group (see Glor & Warren, 2011 for a similar approach), one taking background points from the whole study area (see above) and the other taking background points only from the backgrounds (i.e. fractions of the study area defined by drawing 100-km buffered minimum convex polygons around the records for groups A and B). Fade by clamping was performed, because the MESS (multivariate environmental similarity surface) maps showed that the model was required to extrapolate into novel LGM environmental conditions (Elith, Kearney & Phillips, 2010).

The most common metric, i.e. the Area under the Receiver Operating Characteristic (ROC) Curve (AUC), was used to evaluate the model performance (Fielding & Bell, 1997). As there was no absence data, the fractional predicted area was used (Phillips et al., 2006). An AUC>0.5 indicates that the model performs better than a random prediction.

Assessing the environmental gradient along the Anatolian diagonal. To assess whether the Anatolian diagonal is associated with a steep environmental gradient, the blob range-breaking test was used. This test was preferred over the linear range-breaking test, because the spatial extent of the union of the records for groups A and B was very elongate (Glor & Warren, 2011). To test whether groups A and B share the same environmental space, two quantitative tests of niche similarity (identity and background tests) were also conducted (Warren et al., 2010). For the background test, background samples were taken from all habitats throughout the regions from where the records for groups A and B were randomly sampled (see above). This allowed me to evaluate how different sets of records for groups A and B and vegetation types affected the results of the niche identity test. That is, while the niche identity test analysed only whether the records for groups A and B used for modelling (Figures 2, 3) experience different climates, the background test analysed whether different sets of records created randomly and repeatedly for groups A and B similarly experience different climates. All of these tests were run, with 200 randomised pseudoreplicates, as implemented in ENMTools version 1.4.4 (http://enmtools.blogspot.com.tr; Warren et al., 2010).

ENMTools quantifies niche similarity using two similar metrics (I and Schoener's D; Warren, Glor & Turelli, 2008) that range from 0 (niches highly divergent) to 1 (niches identical). Similar results were obtained from I and Schoener's D metrics in all comparisons, and therefore my discussion was focused on I. To estimate the amount of overlap between areas of above chosen logistic values (i.e. threshold values of 0.2 and 0.3) for groups A and B, the range overlap test was also used, as implemented in ENMTools (see above). All of the GIS operations were conducted using the software SDMtoolbox version 1.1c (Brown, 2014; www.sdmtoolbox.org) and some other tools implemented in the software ArcGIS version 10.1 (www.arcgis.com).

Results

For the whole study area, AUC for test data is AUC=0.935±0.016 (mean ± SD) for group A and AUC=0.916±0.029 for group B. For the backgrounds, AUC for test data is AUC=0.759±0.040 for group A and AUC=0.749 ±0.035 for group B. The ecological niche models performed better than a random prediction, indicating a good fit between the models and test data. The small SDs suggested that the model performance is robust to variation in the selection of the records for training and testing.
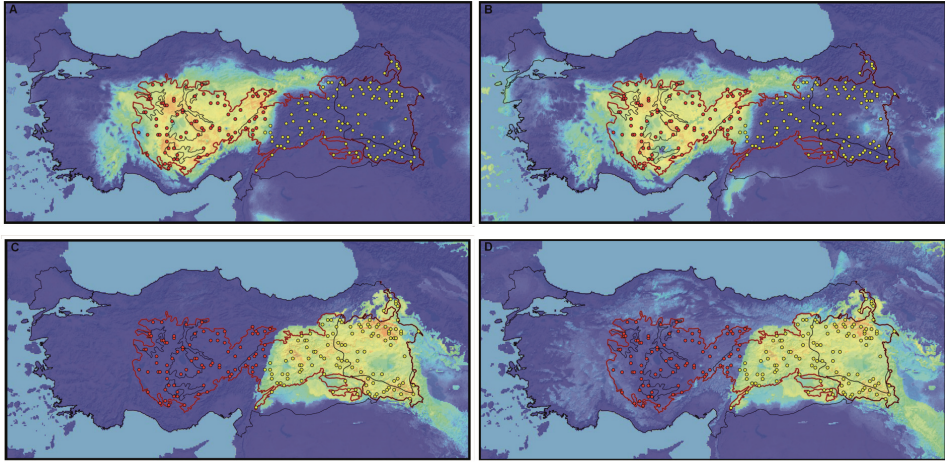
Figure 2.   The ecological niche models for (A, B) group A (red circles) and (C, D) group B (yellow circles) under present (1950–2000) environmental conditions. The models took background points from (A, C) the whole study area or (B, D) the backgrounds. Warmer colours (more red) indicate relatively high logistic values.
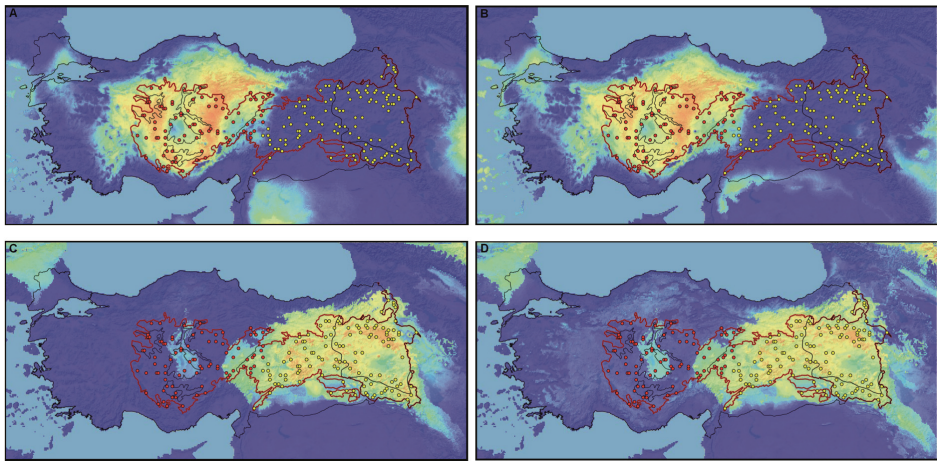

Figure 3.   The ecological niche models for (A, B) group A (red circles) and (C, D) group B (yellow circles) under LGM (about 22,000 years ago) environmental conditions. The models took background points from (A, C) the whole study area or (B, D) the backgrounds. Warmer colours (more red) indicate relatively high logistic values.

For groups A and B, areas of relatively high logistic values were predicted for both the LGM and the present in the west (i.e. central Anatolia) and east (i.e. eastern Anatolia) of the Anatolian diagonal, respectively. The models taking background points only from the backgrounds gave qualitatively similar predictions; i.e. for groups A and B, areas of very low logistic values were predicted for both the LGM and the present in the east and west of the Anatolian diagonal, respectively (Figures 2, 3). The range overlap test supported these results, and indicated that for groups A and B areas of relatively high logistic values had very little overlap at both the LGM (≤7.2% for threshold value 0.2 and ≤0.2% for threshold value 0.3) and the present (≤1.1% for threshold value 0.2 and 0% for threshold value 0.3).
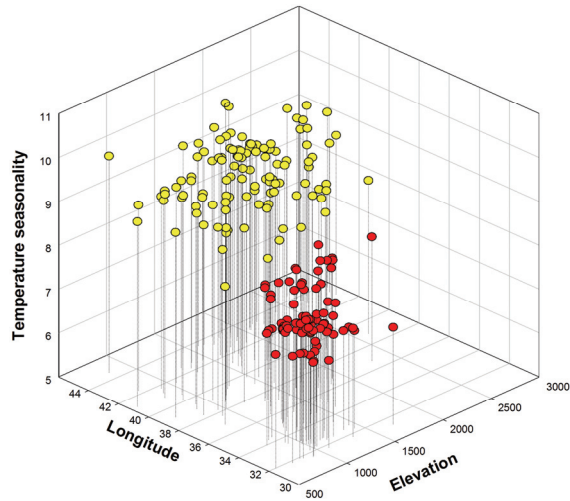
Figure 4.   Plot of the records for group A (red circles) and group B (yellow circles) in a geo-graphical/environmental space defined by longitude (decimal degree), elevation (m), and tempera-ture seasonality (°C).
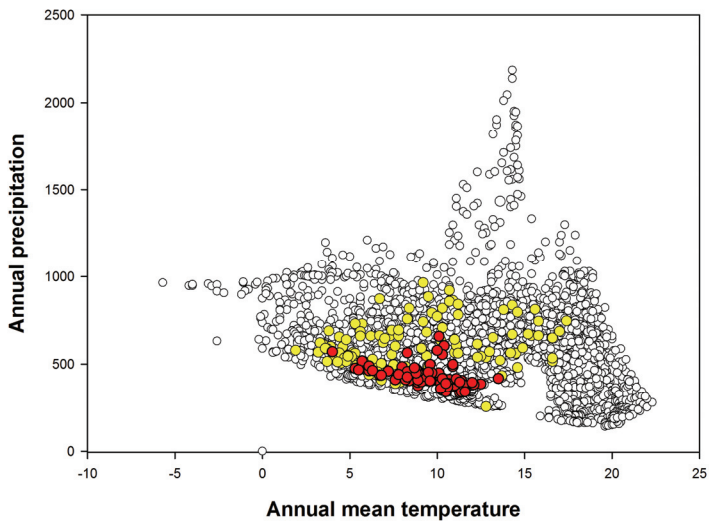

Figure 5.   Plot of the records for group A (red circles) and group B (yellow circles) in an envi-ronmental space defined by annual mean temperature and annual precipitation. White circles indicate environmental conditions present across the study area, based on 5000 random points.

The jack knife analysis suggested that for groups A and B the most significant bio-climatic variable in the models was temperature seasonality (BIO4; i.e. the amount of temperature variation over the course of the year, based on the SD of mean monthly temperature values). The marginal response curves indicated that for group A, logistic values decrease sharply as temperature seasonality goes above 7.5°C, and for group B, logistic values increase sharply as temperature seasonality goes above 8°C. Elevation and temperature seasonality increase towards the east, and therefore are higher for group B than for group A (Figure 4).
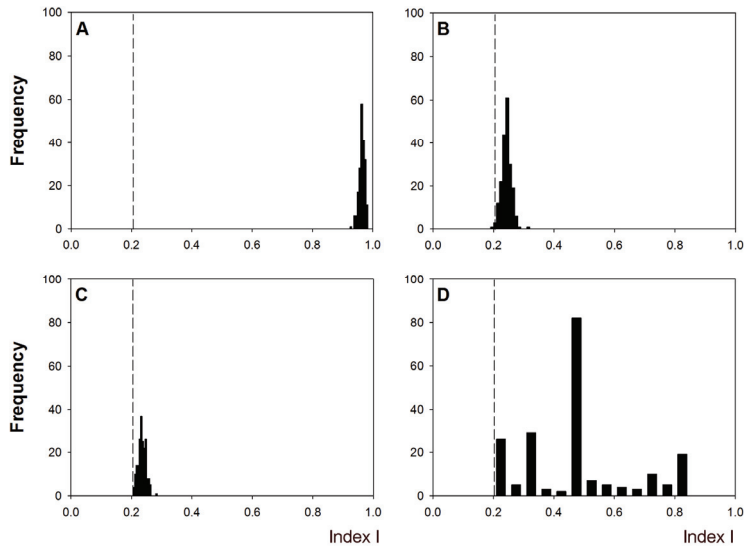
Figure 6.   The frequency distributions of *I* values computed from randomized pseudoreplicates for (A) the niche identity test, (B, C) the background test (B, group A vs. B background; C, group B vs. A background), and (D) the blob range-breaking test. The broken line indicates the observed *I* value (I=0.231).

The identity test indicated that groups A and B do not share the same environmental space (P<0.005; Figures 5, 6). The background test suggested that this result was robust to different sets of records for groups A and B and vegetation types, because the observed *I* value computed from the records for groups A and B used for modelling (see Figures 2, 3) was similar to *I* values computed from different sets of records created randomly and repeatedly for groups A and B (group A vs. B background, P>0.05; group B vs. A background, P>0.05). The blob range-breaking test supported these results, and indicated that environmental divergence is greater between group A and group B than might be expected from randomized geographic breaks (P<0.005; Figure 6), suggesting that the Anatolian diagonal is associated with a steep environmental gradient. This steep gradient associated with the Anatolian diagonal is mainly in temperature seasonality (see above).

Discussion

In this study, using ecological niche modelling and associated comparative metrics, I aimed to assess whether the Anatolian diagonal corresponds with a significant environmental barrier. This, or a similar, approach was proposed by Glor and Warren (2011): "Simple extensions of our framework would permit application to entire faunas or floras separated by biogeographic boundaries. One might, for example, draw background samples from the regions separated by a biogeographic boundary and develop ENMs from these samples to ask whether these areas are more different than expected by chance." Still, this approach (i.e. creating virtual records and splitting these records into two groups by the Anatolian diagonal) can be criticized. However, groups A and B represent some pairs of populations or taxa separated by the Anatolian diagonal and some populations or taxa distributed on only one side of it (see Ekim & Güner, 1986;
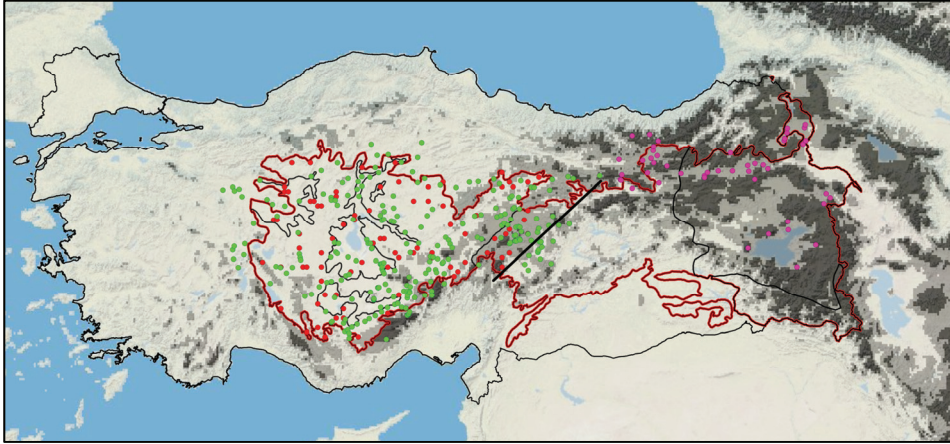
Figure 7.   The geographic distributions of central (lineages 2 to 5; green circles) and eastern (lineage 1 and one unnamed lineage; pink circles) Anatolian lineages of the Anatolian Ground Squirrel (*Spermophilus xanthoprymnus*). Red circles indicate the records for group A. See Figure 1 for other explanations.

Çıplak et al., 1993). For example, the geographic distribution of central Anatolian lineages (no. 2 to 5) of the Anatolian Ground Squirrel (*Spermophilus xanthoprymnus*) almost exactly matches that of group A (Gündüz et al., 2007; Gür, 2013; Figure 7), and the geographic distribution of Radde's Accentor (*Prunella ocularis*) in Anatolia almost exactly matches that of group B (BirdLife International, 2012). Moreover, even though groups A and B do not represent real situations, this approach is a more conservative procedure. If statistically significant results were found using groups A and B that cover the full range of different climates in the west and east of the Anatolian diagonal, respectively, then statistical significance would most probably be found using real populations or taxa, because, in general, they would be more limited distributions and would therefore cover a smaller range of different climates in the west and/or east of it.

The result that the Anatolian diagonal is associated with a steep environmental gradient, and therefore corresponds with a significant environmental barrier is in contrast to the discussion of Davis (1971), and is not surprising given that the Anatolian diagonal forms the boundary both between the central Anatolian and eastern and southeastern Anatolian climate zones (Unal, Kındap & Karaca, 2003) and between ecoregions (Welch & Kirwan, 2008; see above). Eastern Anatolia is one of the best examples of continental collision, and comprises one of the high plateaus of the Alpine-Himalaya mountain belt, with an average elevation of approximately 2000 m (Keskin, 2007). Thus, it is colder and more seasonal, and has higher precipitation, than central Anatolia. Indeed, the most significant bioclimatic variable in the models was temperature seasonality. Also, these two regions host different ecoregions (Welch & Kirwan, 2008; see above). Consequently, the Anatolian diagonal coincides with the distributional limits of many populations (e.g. lineages) or taxa (e.g. species or subspecies; see "Introduction" section). It is also interesting to note that the geographic distributions of hotspots for nitidulid beetles and butterflies are concentrated mostly east of the Anatolian diagonal (Fattorini, Dennis & Cook, 2011, 2012). The models, especially those taking background points only from the backgrounds, did not cross-predict each other, either at the LGM or at the present, suggesting that during at least the last glacial-interglacial cycle,

many of these populations or taxa are excluded from the other side of the Anatolian diagonal by environmental rather than non-environmental reasons (i.e. dispersal, competition). This suggests that the Anatolian diagonal may also have been a significant environmental barrier during the last glacial period (including the LGM). However, all of these explanations do not exclude the possibility that the Anatolian diagonal serves primarily as a geophysical barrier to taxa with low ability of dispersal.

The Anatolian diagonal has an elevation higher than 1500 m and generally less than 2000 m (see Figure 1). The geographic distribution of the Anatolian Ground Squirrel ranges from approximately 800 to 2900 m (Kart Gür & Gür, 2010). Central Anatolian lineages (no. 2 to 5) extend eastwards as far as, but not crossing, the Anatolian diagonal, and are therefore parapatric with eastern Anatolian lineages (1 and one unnamed lineage) in the north of it (Gündüz et al., 2007; Gür, 2013; Figure 7). This suggests that this distribution pattern is mainly shaped by environmental factors (see Gür, 2013 for the results of ecological niche modelling on the species). However, many Orthoptera species that are wingless or with vestigial wings show the Anatolian diagonal-specific distributions because they have a low ability for dispersal (Çıplak et al., 1993).

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Disclosure Statement

References

Adıgüzel, N. (1999): A new species of *Astragalus* (Fabaceae) from East Anatolia, Turkey. *Annales Botanici Fennici, 36*, 231–233.

Avcı, M. (1993): Türkiye'nin flora bölgeleri ve Anadolu Diagonali'ne coğrafi bir yaklaşım [Flora regions of Turkey and a geographical approach to the Anatolian Diagonal]. *Türk Coğrafya Dergisi, 28*, 225–248.

Aydın, S. (2004): Anadolu Diyagonali: ekolojik kesinti tarihsel-kültürel bir farklılığa işaret edebilir mi? [The Anatolian Diagonal: can ecological barrier indicate a historical-cultural difference?]. *Kebikeç, 17*, 117–137.

Bilgin, R. (2011): Back to the suture: the distribution of intraspecific genetic diversity in and around Anatolia. *International Journal of Molecular Sciences, 12*, 4080–4103.

BirdLife International. (2012): *Prunella ocularis*. The IUCN Red List of Threatened Species. Version 2015.2. <www.iucnredlist.org>. Downloaded on 30 June 2015

Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson, R. P. (2014): Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling, 275*, 73–77.

Brown, J. L. (2014): SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution, 5*, 694–700.

Conservation International (2015): Conservation International: Biodiversity Hotspots – Europe and Central Asia. www.cepf.net/resources/hotspots (accessed 28 May 2015).

Çıplak, B. (2003): Distribution of Tettigoniinae (Orthoptera, Tettigoniidae) bush-crickets in Turkey: the importance of the Anatolian Taurus Mountains in biodiversity and implications for conservation. *Biodiversity and Conservation, 12*, 47–64.

Çıplak, B., Demirsoy, A., & Bozcuk, A. N. (1993): Distribution of Orthoptera in relation to the Anatolian diagonal in Turkey. *Articulata, 8,* 1–20.

Davis, P. H. (1971): Distribution patterns in Anatolia with particular reference to endemism. Pp. 15–27. In: Davis, P. H., Harper, P. C., & Hedge, I. C. (Eds.), *Plant Life of South-West Asia*. Edinburgh: The Botanical Society of Edinburgh.

Demirsoy, A., Salman, S., & Sevgili, H. (2002): *Novadrymadusa*, a new genus of bushcricket with a new species and notes on related genera (Orthoptera: Tettigoniidae). *Journal of Orthoptera Research, 11*, 175–183.

Doğan, B., Duran, A., & Hakkı, E. (2009): Numerical analyses of wild *Jurinea* spp. (Asteraceae) in Turkey. *Bangladesh Journal of Botany, 38*, 47–53.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013): Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*, 27–46.

Eken, G., Evans, M., Karataş, A., Balkız, Ö., Karaçetin, E., Kılıç, T., … Karataş, A. (2004): Irano-Anatolian. Pp. 287–295. In Mittermeier, R. A., Gil, P. R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., … Da Fonseca, G. A. B. (Eds.), *Hotspots Revisited*. Mexico: CEMEX.

Ekim, T., & Güner, A. (1986): The Anatolian diagonal: fact or fiction? *Proceedings of the Royal Society of Edinburgh, Section B, Biological Sciences, 89*, 69–77.

Elith, J., Kearney, M., & Phillips, S. (2010): The art of modelling range-shifting species. *Methods in Ecology and Evolution, 1,* 330–342.

Elith, J., & Leathwick, J. R. (2009): Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics, 40*, 677–697.

Fattorini, S., Dennis, R. L. H., & Cook, L. M. (2011): Conserving organisms over large regions requires multi-taxa indicators: one taxon's diversity-vacant area is another taxon's diversity zone. *Biological Conservation, 144*, 1690–1701.

Fattorini, S., Dennis, R. L. H., & Cook, L. M. (2012): Use of cross-taxon congruence for hotspot identification at a regional scale. *PLoS ONE,* 7(6), e40018.

Fielding, A. H., & Bell, J. F. (1997): A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation, 24*, 38-49.

Fourcade, Y., Engler, J. O., Rodder, D., & Secondi, J. (2014): Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PLoS ONE,* 9(5), e97122.

Glor, R. E., & Warren, D. (2011): Testing ecological explanations for biogeographic boundaries. *Evolution, 65*, 673–683.

Gündüz, I., Jaarola, M., Tez, C., Yeniyurt, C., Polly, P. D., & Searle, J. B. (2007): Multigenic and morphometric differentiation of ground squirrels (*Spermophilus*, Sciuridae, Rodentia) in Turkey, with a description of a new species. *Molecular Phylogenetics and Evolution, 43*, 916–935.

Gür, H. (2013): The effects of the late Quaternary glacial-interglacial cycles on Anatolian ground squirrels: range expansion during the glacial periods? *Biological Journal of the Linnean Society, 109*, 19–32.

Hansen, M., DeFries, R., Townshend, J. R. G., & Sohlberg, R. (1998): UMD Global Land Cover Classification, 1 Kilometer, 1.0. Department of Geography, University of Maryland, Maryland.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005): Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology, 25*, 1965–1978.

Kapli, P., Botoni, D., Ilgaz, Ç., Kumlutaş, Y., Avcı, A., Rastegar-Pouyani, N., Fathinia, B., Lymberakis, P., Ahmadzadeh, F., & Poulakakis, N. (2013): Molecular phylogeny and historical biogeography of the Anatolian lizard *Apathya* (Squamata, Lacertidae). *Molecular Phylogenetics and Evolution, 66*, 992–1001.

Kart Gür, M., & Gür, H. (2010): *Spermophilus xanthoprymnus* (Rodentia: Sciuridae). *Mammalian Species, 42*, 183–194.

Keskin, M. (2007): Eastern Anatolia: a hotspot in a collision zone without a mantle plume. *Geological Society of America Special Papers, 430*, 693–722.

Korkmaz, E. M., Lunt, D. H., Çıplak, B., Değerli, N., & Başıbüyük, H. H. (2014): The contribution of Anatolia to European phylogeography: the centre of origin of the meadow grasshopper, *Chorthippus parallelus*. *Journal of Biogeography*, 41, 1793–1805.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder, B., Lindenborn, J., Reinfelder, V., … & Wilting, A. (2013): The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions, 19*, 1366–1379.

Mittermeier, R. A., Gil, P. R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., … Da Fonseca, G. A. B. (Eds.). (2004): *Hotspots Revisited*. Mexico: CEMEX.

Mutun, S. (2010): Intraspecific genetic variation and phylogeography of the oak gallwasp *Andricus caputmedusae* (Hymenoptera: Cynipidae): effects of the Anatolian diagonal. *Acta Zoologica Academiae Scientiarum Hungaricae, 56*, 153–172.

Nilson, G., Andren, C., & Flardh, B. (1990): *Vipera albizona*, a new mountain viper from central Turkey, with comments on isolating effects of the Anatolian "Diagonal". *Amphibia-Reptilia, 11*, 285–294.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006): Maximum entropy modeling of species geographic distributions. *Ecological Modelling, 190*, 231–259.

Phillips, S. J., & Dudik, M. (2008): Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography, 31*, 161–175.

Rokas, A., Atkinson, R. J., Webster, L., Csóka, G., & Stone, G. N. (2003): Out of Anatolia: longitudinal gradients in genetic diversity support an eastern origin for a circum-Mediterranean oak gallwasp *Andricus quercustozae*. *Molecular Ecology, 12*, 2153–2174.

Şekercioğlu, Ç. H., Anderson, S., Akçay, E., Bilgin, R., Can, Ö. E., Semiz, G., … Dalfes, H. N. (2011): Turkey's globally important biodiversity in crisis. *Biological Conservation, 144*, 2752–2769.

Sonibare, M. A., Armagan, M., Özgökce, F., Yaprak, A. E., Mayland-Quellhorst, E., & Albach, D. C. (2014): Analysis of taxonomic and geographic patterns of Turkish *Veronica orientalis* using nuclear and plastid DNA and morphological data. *Plant Systematics and Evolution, 300*, 645–664.

Stümpel, N., & Joger, U. (2009): Recent advances in phylogeny and taxonomy of Near and Middle Eastern Vipers – an update. *ZooKeys, 31*, 179–191.

Unal, Y., Kındap, T., & Karaca, M. (2003): Redefining the climate zones of Turkey using cluster analysis. *International Journal of Climatology, 23*, 1045–1055.

Uslu, E., & Bakış, Y. (2012): Geographic distribution of Turkish oaks. *Dendrobiology,* 67, 41–48.

Uslu, E., Bakış, Y., & Babaç, M. T. (2011): A study on biogeographical distribution of Turkish oak species and their relations with the Anatolian diagonal. *Acta Botanica Hungarica, 53*, 423–440.

Vamberger, M., Stuckas, H., Ayaz, D., Gracia, E., Aloufi, A. A., Els, J., … Fritz, U. (2013): Conservation genetics and phylogeography of the poorly known Middle Eastern terrapin *Mauremys caspica* (Testudines: Geoemydidae). *Organisms Diversity and Evolution, 13*, 77–85.

Warren, D. L., Glor, R. E., & Turelli, M. (2008): Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution, 62*, 2868–2883.

Warren, D. L., Glor, R. E., & Turelli, M. (2010): ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography, 33*, 607–611.

Welch, H., & Kirwan, G. M. (2008): Turkey's ecoregions: their biodiversity and conservation. Pp. 31–41. In: Kirwan, G., Demirci, B., Welch, H., Boyla, K., Özen, M., Castell, P., & Marlow, T. (Eds.), *The Birds of Turkey.* London: Helm.